

New brachyuran crabs (Crustacea: Decapoda) from the Upper Pliocene Yorktown Formation of southeastern Virginia

Warren C. Blow

Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20013-7012, U.S.A.

Abstract.—Six new species of crabs, representing three families and one new genus, are described and illustrated from the Upper Pliocene Yorktown Formation of southeastern Virginia. They are remarkable for their state of preservation and represent the first fossil record for three of these living genera in Virginia's rich Neogene marine deposits. The presence of *Stenocionops* along with the common occurrence of *Persephona* in these deposits suggests that warm temperate waters covered southeastern Virginia during the deposition of late Yorktown sediments.

Introduction

In 1935, Mary J. Rathbun published the first comprehensive paper on the fossil crustaceans, principally decapods, of the Atlantic Gulf Coastal Plain of Eastern North America. In this landmark paper she describes or mentions all of the fossil decapod, stomatopod and isopod crustaceans from this region made available to her at that time from a host of sources (Rathbun 1935:1). Of the 25 families, 67 genera, and 167 species covered, and for the most part illustrated, in her paper only eight species representing six genera and six families were listed and treated from Virginia from deposits of Miocene, Pliocene and Pleistocene age. All but one were listed as occurring in deposits of the Yorktown Formation which at that time was regarded as Miocene. However the Neogene stratigraphy of southeastern Virginia has evolved considerably since 1935 (Hazel 1971a, Ward & Blackwelder 1980, Ward & Gilinsky 1993), and consequently only *Cancer borealis* Stimpson, 1859, *Panopeus herbstii* Milne-Edwards, 1834, and *Libinia dubia* Milne-Edwards, 1834, are listed from localities that are now regarded as old as Miocene.

With the exception of *Cancer borealis*

Stimpson, 1859, the remaining species—*Callianassa suffolkensis* Rathbun, 1935; *C. atlantica* Rathbun, 1926; *Persephona punctata* (Linné, 1758); *Callinectes sapidus* Rathbun, 1896; *Panopeus herbstii* Milne-Edwards, 1834; and *Libinia dubia* Milne-Edwards, 1834—are all listed from localities now regarded as Upper Pliocene. *Callinectes sapidus* Rathbun, 1896 is the only species listed from the Pleistocene.

In the present paper six additional taxa, *Hepatus bottomsii*, n. sp., *Pterocarcinus baileyi*, n. gen, n. sp., *Persephona niemeyeri*, n. sp., *P. rodesae*, n. sp., *Stenocionops dyeri*, n. sp., and *Euprognatha ricei*, n. sp. are described as new and illustrated from deposits of late Pliocene age in the same general geographic area as that treated by Rathbun 67 years ago. Unlike Rathbun's material, which is very fragmentary, often consisting only of fingers, the taxa presented in this paper are remarkable for their state of preservation and completeness. All are represented by their original exoskeleton, and many even exhibit a uniform color similar to that of their living relatives.

The material studied in this paper was collected from the Moore House Member of the upper part of the Yorktown Formation from three localities in southeastern

Virginia. They are: The Lone Star Lakes, near Chuckatuck, Suffolk; Riddick Pit, borrow pit east side Virginia Routes 10/32, 4.4 km southeast of Benns Church; and Rices Pit, a now flooded borrow pit in Hampton (Ward & Blackwelder 1980). Detailed locality data for these localities are provided in Appendix 1.

With the exception of one female paratype of *Stenocionops*, the gender of the remaining specimens described in this paper could not be determined.

Stratigraphy & Paleoenvironment

Mansfield (1943) expanded on his earlier biostratigraphic division of the Yorktown Formation into Zones I and II and regarded both units as entirely Miocene. His zonation, though flawed, was very workable in the field for many years. Hazel (1971a) divided the Yorktown into three ostracode zones of which the uppermost or *Puriana mesacostalis* zone, he regarded as Pliocene. Ward & Blackwelder (1980) refined the stratigraphy of the Yorktown Formation by redefining and dividing it into two formations: the Upper Miocene Eastover Formation overlain by the Lower Pliocene Yorktown Formation. The latter was further divided into four members which in ascending order were named: Sunken Meadow, Rushmere, Mogarts Beach, and Moore House. Ward & Blackwelder (1980:44), in defining the uppermost member state, "the Moore House Member, representing the regressive phase of the Yorktown Formation, reflects a renewal of higher current and wave energy conditions. The member consists of sandy shell beds and cross-bedded shell hash and locally is cemented to form a very indurated rock." They further (p. 45, 47) state, "The Moore House Member is found only east of the Surry Scarp," and "The Moore House Member reflects a progressively shallowing, regressive sea. Molluscan assemblages indicate normal salinities, but some of the highest beds in the Williamsburg area contain a few brackish-

water mollusks. Locally large offshore bars were the site of rapid, large-scale, cross-bedded sand deposition." All of the specimens studied in this paper and the strata at the localities from which they were derived are now regarded by L. W. Ward as belonging to the Moore House Member and of late Pliocene age (Ward, pers. comm., 26 November 2002). Kier (1972), in a study of the echinoids from two (Chuckatuck and Rices Pit) of the three localities covered in this paper, gives a late Miocene age for his material. This age, though now regarded as incorrect, was based on the ostracode zones of Hazel (1971a) and the work of Gibson (1967). A late Miocene age for strata found at these localities was also the consensus of Neogene molluscan workers at that time. Kier's interpretation of the life habits of the Yorktown echinoids is a valuable resource for understanding the paleoenvironmental conditions that existed during the deposition of the Yorktown at Rices Pit and particularly at the Chuckatuck Bar. (See Johnson & Coch 1969, Johnson 1969 and Campbell 1993 for a detailed description of the structure, extent and mollusks of the Chuckatuck Bar, which includes the deposits at the Riddick Pit).

Kier (1972:3) states, "The Yorktown echinoids, like the ostracodes, indicate a past climate warmer than now" . . . "Although some of these living species range into cooler waters, they all occur in subtropical regions, suggesting that the fossil echinoids they resemble lived in waters warmer than the mild-temperate waters now occurring off the coast of Virginia" Earlier, Hazel (1971b) in a detailed study of the Yorktown ostracodes coupled with his own detailed studies of Western Atlantic Recent ostracodes concluded that the climate of the Yorktown Sea was much warmer than Virginia's coastal waters are today. Kier (1972: 2) in summarizing Hazel (1971b) states, "This equable thermal regime is markedly different from that of any province and concomitant climate zone now extant along the Atlantic coast of the United States. The

temperatures varied from about 12°C to 15°C in the winter to about 17.5°C to 20°C and finally to 20°C to 25°C in summer.” Ward & Gilinsky (1993:26) state, “The Yorktown Sea supported a large, warm-temperate to subtropical molluscan assemblage.” Western Atlantic species of the spider crab *Stenocionops* are not reported north of Cape Hatteras, North Carolina but inhabit warmer waters further south, some to Brazil (see Rathbun 1925; Williams 1965, 1984 for geographic ranges). The purse crab, *Persephona mediterranea* (Herbst, 1794) though reported from as far north as New Jersey and the southern Chesapeake Bay, is not commonly found there but is commonly found in warmer more southern waters from off Cape Hatteras to Brazil. The crabs of the Yorktown Sea, like the mollusks and other invertebrates found at the localities cited here, are representative of similar taxa that would be found today in warm-temperate to subtropical, open marine waters of normal salinity.

Terms and Conventions

The minute mushroom-shaped structures found on the surfaces of numerous brachyurans, and referred to by French authors for more than 100 years as “champignons” (mushrooms) in reference to their “mushroom-like” appearance, are here referred to as bolitimorphs after the Greek bolites (mushroom) in combination with the Greek morphe (form, shape). Bolitimorph as here defined is intended to replace the phrases “mushroom-like structure” or “mushroom-shaped structure”. At least one living species, *Merocryptus boletifer* Milne-Edwards & Bouvier, 1894, from the Azores was named for this common feature.

Haj & Feldmann (2002) observed similar structures in members of the family Raninidae and introduced the term “fungiform” for their mushroom shaped structures that form a “pebbled surface” and stated, “This pebbled surface has not been recognized in any other decapod taxon, nor

has its structure and function been described previously.” These structures have, however been known for some time as noted above, and both their development and function studied in great detail (Serène 1954, Guinot 1979). Given the vast range of shapes suggested by the term Fungi, the term bolitimorph is more specific and is preferred here to denote mushroom-shaped structures.

Repositories.—Primary and secondary types are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, and The Virginia Museum of Natural History, Martinsville, Virginia as indicated.

Abbreviations.—NMNH, National Museum of Natural History, Smithsonian Institution; S.I., Smithsonian Institution; USGS, U.S. Geological Survey (when used with number indicates a locality; see locality register at end of paper); USNM, abbreviation for catalogue numbers of the former U.S. National Museum now the National Museum of Natural History; VMNH, Virginia Museum of Natural History.

Measurements

Measurements are expressed in millimeters. Abbreviations are as follows: cl, carapace length, maximum longitudinal measurement; cw, maximum transverse measurement; prl, propodus length, length of palm or combined length of palm and fixed finger; prh, propodus height; prt, propodus thickness.

Systematic Paleontology

Family Calappidae

Subfamily Matutinae

Genus *Hepatus*, Latreille, 1802

Hepatus bottomsii, new species

Fig. 1

Diagnosis.—Carapace arcuate (shaped like a drawn bow), front prominent, strongly elevated, produced well beyond orbits and anterolateral margin; dorsal surface

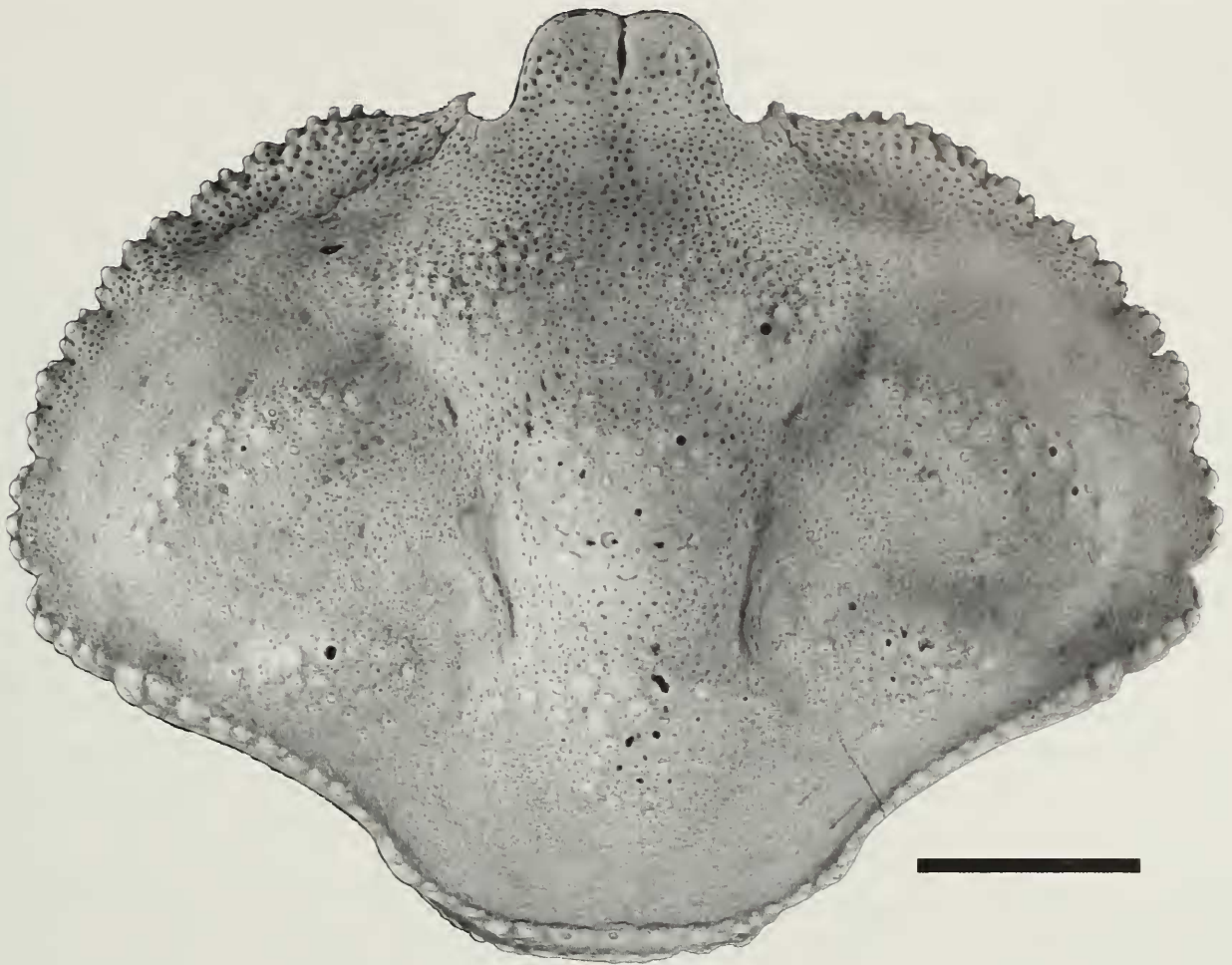


Fig. 1. *Hepatus bottomsii* Holotype (USNM 520705) dorsal view. Scale = 10 mm.

with eight distinct, pustulate protuberances; suborbital flank deeply depressed above descending, weakly sinuous anterolateral margin; surfaces everywhere pitted, particularly anteriorly where appearing eroded.

Description.—Carapace arcuate, strongly narrowing posteriorly, broad, length about three-fourths width, widest just forward of anterior-lateral angle, strongly convex longitudinally and highly arched transversely, appearing tripartite in frontal view, gastric and branchial regions distinctly swollen, regions moderately well defined, greatly elevated in younger individuals; dorsal surface with eight prominent, pustulate protuberances. Surfaces everywhere pitted, giving an eroded appearance; pits most abundant on anterior one-third of carapace particularly on front, eyes, orbits, post orbital and anterolateral margins, and adjacent surfaces. Surfaces somewhat smoother in larger, more mature individuals. Fronto-orbital

width between one-fourth and one-third carapace width. Front prominent, thick, bilobate, strongly projecting beyond orbits and anterolateral margin (and placed well above anterolateral continuation of borders of carapace); lobes truncate with lateral margins rounded anteriorly, dorsally divided by deep sulcus, ventrally fused or closed along entire length. Antennules very obliquely set. Orbit small, subcircular, defined by slightly raised wide rim; rim composed of three lobes, base of eye in orbit level with front; orbits directed obliquely downward parallel to slope of thick, rounded dorsal margin above suborbital depression. Anterolateral margin comprised of about 40 blunt denticles situated on from 12 to 13 or more teeth; teeth separated by closed incisions, most of which begin with a deep pit; teeth bidentate anteriorly otherwise most often tridentate with median denticle strongest. Margin, where descending

anteriorly to buccal cavity, weakly sinuous, comprised of single row of denticles of subequal strength. Posterolateral margin straight, strongly convergent posteriorly; anterior portion of margin, just posterior to strong tooth defining anterolateral angle, with a long low-angle tooth directed obliquely forward, tooth with double or triple close set rows of low tubercles; tubercles continue as a single or double row to distinct, though small, subacute tooth defining posterolateral angle; single row of tubercles continue transversely across posterior margin of carapace where it eventually continues along the opposing lateral margins until returning to the opposite side of the buccal cavity from which it began. Posterior margin high, narrow, width about one-seventh to one-fifth carapace width; margin defined above by slightly convex row of tubercles continuous with row of posterolateral margin, and submarginal row of tubercles below. Postfrontal surface with medial, broad, very shallow sulcus leading to base of frontal lobes. Epigastric region defined by minute pustules on either side of base of postfrontal sulcus. Hepatic region depressed, bordered anteriorly by thick, rounded carapace margin leading to orbit. Remaining dorsal regions defined by eight prominent, pustulate protuberances distributed as follows: paired protogastric, one mesogastric, one cardiac, paired epibranchial, and paired mesobranchial. Protogastric and mesogastric regions large, of subequal size, subcircular. Epibranchial regions developed into oblique ridges directed toward marginal tooth of anterolateral angle. Mesobranchial regions developed into ridges aligned roughly with anterior ridge of cardiac region to form a transverse line of protuberances aligned with first posterolateral tooth. Anterior face of ridges, smooth, steep. Intestinal region weakly inflated, indistinct. Posterior gastric pits minute, closely spaced.

Color.—Rust or yellowish brown to brownish gray when dry, gray or dark gray

when wet. Recent species in alcohol are usually gray.

Etymology.—This species is named for E. Edward Bottoms, paleoanthropologist of Portsmouth, Virginia, in recognition of his numerous writings on Paleo Indians of the Eastern United States, for his years of teaching regional history on all student levels in the Tidewater Area, and for stimulating the author's early interest and development in paleontology.

Holotype.—The Lone Star Lakes, near Chuckatuck, Suffolk, Virginia. USGS 26891; (USNM 520705) cl 42.88 mm, cw 54.92 mm. *Paratypes*: (USNM 520706), cl 49.97 mm, cw 66.18 mm. USGS 26891 as above; (USNM 520707), cl 33.63 mm, cw 42.77 mm. USGS 26891 as above. (VMNH I3546), cl 47.24 mm, cw 64.19 mm. Same geographic locality as USGS 26891 as above.

Occurrence.—The Lone Star Lakes, near Chuckatuck, Suffolk, Virginia.

Remarks.—Recent comparisons: The greatly produced front of *H. bottomsii* immediately separates it from all living species of *Hepatus* but may confuse it with species of the genus *Hepatella*, Smith, in Verrill, 1869, type species *H. amica*, from which it differs as follows. Adult specimens of *Hepatus bottomsii* have eight low dorsal protuberances compared to the six greatly elevated dorsal protuberances found in adults of *Hepatella*, and as Rathbun, 1937 notes, *Hepatella* lacks the suborbital depression found in members of the genus *Hepatus*. This feature is distinct in *H. bottomsii*.

Fossil comparisons: *Hepatus bottomsii* differs from the middle Miocene *H. nodosus* Collins & Morris, 1976, of Trinidad, the only fossil species with which it might be confused, in having a greatly produced front and obliquely directed epibranchial ridges. In *H. nodosus* the front is marginal and the epibranchial ridges are transverse.

Individuals of *H. bottomsii* become smoother and their dorsal protuberances

lower and much less pronounced as they grow larger and older.

Leucosiidae
Subfamily Ebalinae
Pterocarcinus, new genus

Diagnosis.—Carapace suboctagonal, wing like; “wing” or branchial region extending laterally well beyond basis of legs; margins very thin, carinate; front narrow with two very weak rostral “horns”; cardiac region most prominent, a raised, subcircular platform or “mesa” surrounded by a deep, wide sulcus; posterior margin broad, bilobate.

Type species.—*Pterocarcinus baileyi*, n. sp. by present designation and monotypy.

Related species.—?*Ebalia rotundata* (A. Milne-Edwards, 1880); See A. Milne-Edwards & E. L. Bouvier, 1902 for figures. Generic status uncertain.

Etymology.—*Ptero* from the Greek, pteron, wing, in combination with the generic name *Carcinus* derived from the Greek, karkinos, or crab. Gender masculine.

Remarks.—In outline *Pterocarcinus* resembles a number of species currently placed in *Ebalia* Leach, 1817; *Lithadia* Bell, 1855 and *Speloeophorus* A. Milne-Edwards, 1865, but it differs dramatically in overall shape and form from the type species of all of these genera. It does not possess the subhemispherical form of the type species of *Ebalia*, *E. tuberosa* (Pennant, 1777). Nor does it exhibit the outline, “thick” wings, and caverns of the type species of *Speloeophorus*, *S. nodosus* (Bell, 1855), and it does not exhibit the highly elevated and excavated form represented by the type of *Lithadia*, *L. cumingii* Bell, 1855. (See Rathbun 1937, for figures of North and South American species placed in these genera). In overall form and outline *P. baileyi* most closely resembles *Ebalia rotundata* (A. Milne-Edwards, 1880), a species clearly not in the genus *Ebalia*, but one which might be its closest living relative. *Ebalia rotundata*, though very similar to

this new species, differs in having very thick or rotund branchial “wings” unlike the thin carinate wings of *Pterocarcinus* and in having the cardiac and urogastric regions joined and not completely separated by a deep sulcus as in *Pterocarcinus* (Fig. 2A). In the absence of the first right pleopod of a male and other features present in living material, the true relationship of this new fossil genus to other leucosiids may never be fully understood, but its form is quite different from all known genera. Fragments of this new genus are fairly common in strata of Pliocene age along the Atlantic Coastal Plain. Given this situation it seems best to give this unusual leucosiid a distinct generic name.

Pterocarcinus baileyi, new species
Figs. 2–4

Diagnosis.—As for genus.

Description.—Carapace suboctagonal, wing-like, length about eight-tenths width, broadest at anterolateral angle; regions moderately well defined; dorsal ridge from front along midline to and including intersecting diagonal branchial ridges; hepatic and cardiac regions and posterior lobes distinct to prominent, ridges greatly elevated; irregular inner margin of elevated hepatic region deeply excavated. Cardiac region most prominent (Figs. 2A, 3B, F), a raised, subcircular or oval free-standing “mesa-like” platform completely surrounded by a deep, wide sulcus filled with scattered, tall bolitimorphs (Fig. 3B, D); “mesa” slightly elevated above ridge of branchial region and strongly produced posteriorly. Most surfaces of carapace covered with pavement of low, closely spaced or abutting bolitimorphs (Fig. 2A); bolitimorphs separate or free standing in depressions adjacent to ridge leading to front, along and anterior to diagonal ridge of branchial region, and in sulcus completely surrounding cardiac “mesa-like” region as well as ventral surfaces of pterygostomian and branchial regions where they are highest and most dis-

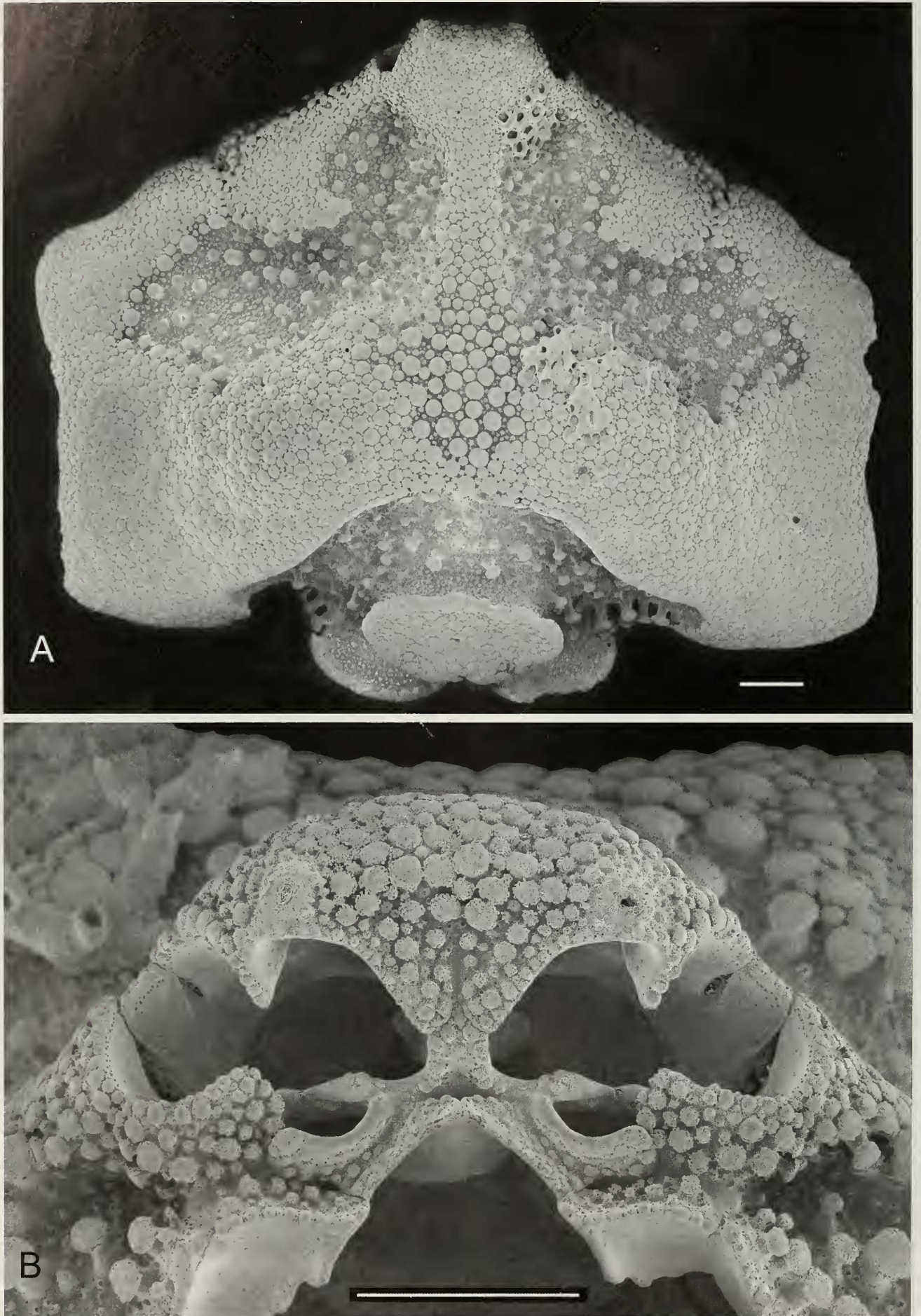


Fig. 2. *Pterocarcinus baileyi* Holotype (VMNH I3547) A. dorsal view; B. frontal view, close up. Scale = 1 mm.

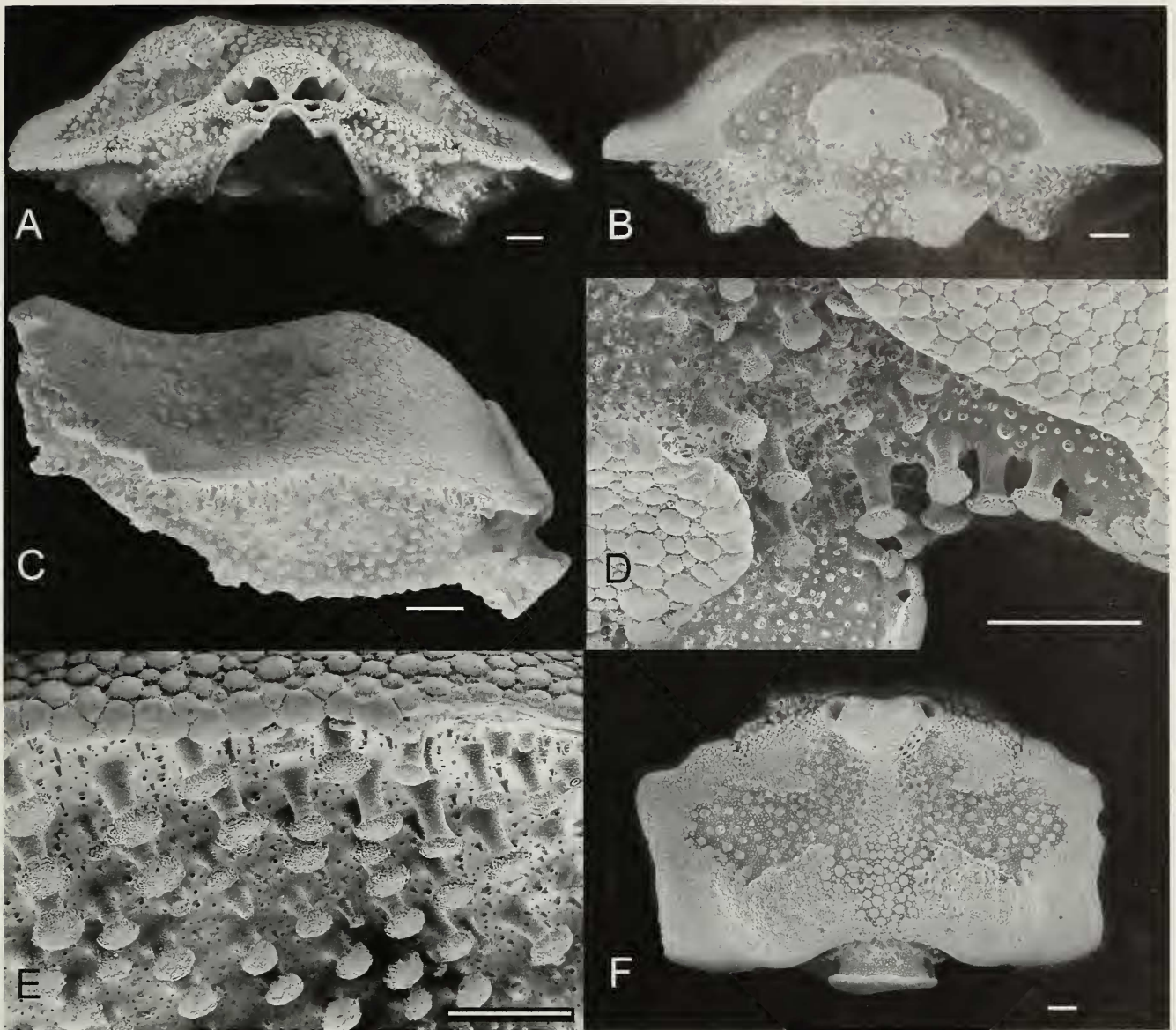


Fig. 3. *Pterocarcinus baileyi* Holotype (VMNH I3547) A. anterior view; B. posterior view; C. left lateral view; D. oblique posterior view. Scale = 1 mm. E. left lateral view of ventral surface beneath branchial "wing". Scale = 0.5 mm. F. oblique frontal view to show height of cardiac "mesa". Scale = 1 mm.

tinct. Front truncate, elevated, narrow, width slightly less than one-sixth width of carapace, lateral margins defined by very short, rounded, blade-like "horns" (Fig. 2A, B); front weakly projecting. Horns appearing more distinct in younger individuals. Fronto-orbital width about one-fourth carapace width. Orbit sub-circular, marginal, with three sutures, slightly produced at ex-orbital margin. Orbit and antennule fossae openly connected; basal antennal segment not present (not preserved); antennule fossae oblique. Bolitimorphs on fronto-orbital surfaces closely spaced forming pavement (Fig. 2B).

Pterygostomian region developed into long ridge subparallel to anterolateral margin (Fig. 3A); ridge composed of free standing rows of bolitimorphs of median length that cluster to form a downward, obliquely directed tooth before terminating posteriorly. Buccal cavity triangular, anterior margins of afferent channels with minute pustules, margin curving downward laterally to a narrow notch or sulcus. Branchial "wings" extending laterally well beyond basis of ambulatory legs and chela (Fig. 3A-C); legs probably not visible in dorsal view. "Wings" ventrally covered with distinctly separated tall bolitimorphs

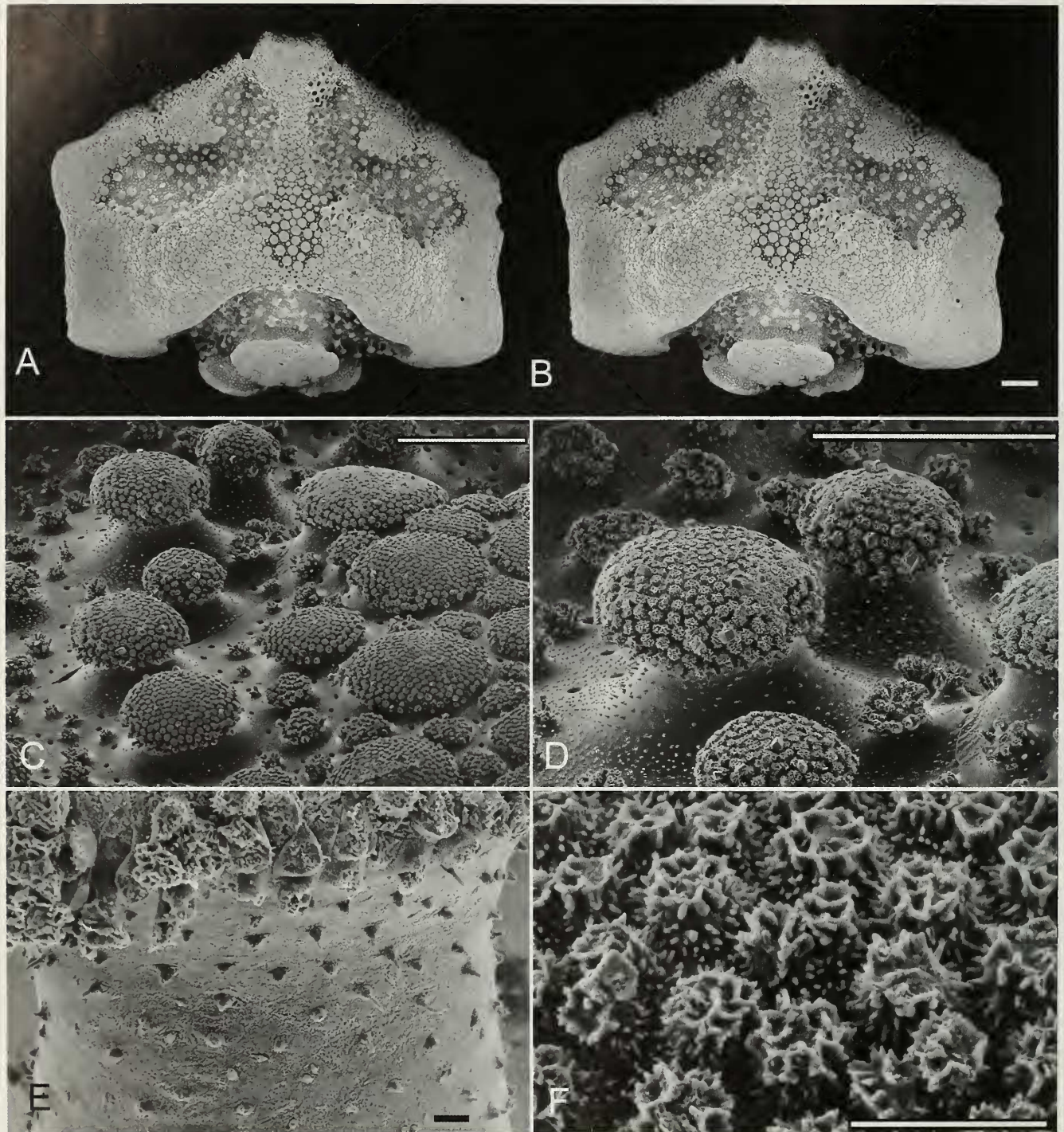


Fig. 4. *Pterocarcinus baileyi* Holotype (VMNH I3547) A., B. stereo pair in dorsal view. Scale = 1 mm. *Pterocarcinus baileyi* Paratype (USNM 520708) C., D. close-up of bolitimorphs in post-hepatic depression. Scale = 200 μm . *Pterocarcinus baileyi* Holotype (VMNH I3547) E. close-up of stalk of bolitimorph to show dagger-like structures that might function to hold sediment in place. Scale = 10 μm . *Pterocarcinus baileyi* Paratype (USNM 520708) F. high magnification to show unique structure of crown of bolitimorph seen in figures C. and D. above. Scale = 20 μm .

(Fig. 3E); bolitimorphs much shorter and abutting around margins at insertion of ambulatory legs and chela. Anterolateral, lateral, and posterolateral margins very thin, carinate (Fig. 3A–C); leading edge of each curving downward like an airfoil; edge ap-

pearing beaded below where bordered by a single row of minute bolitimorphs. Anterolateral margin longest, convergent anteriorly, set at 40 degrees to longitudinal axis; margin interrupted medially by a very distinct fissure between hepatic and branchial

regions; margin anterior to fissure thickened and posterior to fissure sinuous; anterolateral angle rounded to subacute. Lateral margin about two-thirds length of anterolateral margin, distinctly concave in dorsal view and raised medially in lateral view; anterior half weakly divergent anteriorly; posterior half subparallel to longitudinal axis and terminating in a subacute angle. Posterolateral margin perpendicular to longitudinal axis, length less than one-half length of anterolateral margin; margin separated from posterior lobes by deep sulcus. Posterior distinctly bilobate, width slightly less than one-half width of carapace; lobes thick, separated by a deep fissure; dorsal surface of each, smooth; lobes moderately produced posteriorly, margin of each terminating in a thin, raised, beaded rim.

Apparent posterior gastric pits distinct, very widely spaced, set on branchial ridges just anterior to gastro-cardiac sulcus (Fig. 2A).

Color.—Brown, buff, or sometimes weathered bluish grey.

Etymology.—This species is named for Richard H. Bailey, geologist and paleontologist, Professor, Northeastern University, Boston, Massachusetts, for his research contributions to Atlantic Coastal Plain geology and paleontology, for his many years of superb teaching, and especially for his years of encouragement and field assistance to the author.

Holotype.—Riddick Pit, about 4.4 km southeast of Benns Church, Isle of Wright County, Virginia. Same geographic locality as USGS 26892 (VMNH I3547), cl 10.04 mm, cw 12.75 mm. *Paratypes*: (VMNH I3548), cl 10.77 mm, cw 13.36 mm estimate, incomplete. Same geographic locality as USGS 26892 above. (USNM 520708), cl 9.16 mm, cw 10.22 mm, USGS 26891, The Lone Star Lakes, near Chuckatuck, Suffolk, Virginia; (USNM 520709), cl 8.79 mm, cw 10.95 mm, USGS 26891 as above.

Occurrence.—Riddick Pit, about 4.4 km southeast of Benns Church, Isle of Wright

Co., Virginia, and The Lone Star Lakes, near Chuckatuck, Suffolk, Virginia.

Remarks.—The function of the boletimorphs found on *Pterocarcinus baileyi* and other crabs probably differs with each of the taxa on which they occur. Given the difficulty of cleaning specimens covered with these boletimorphs, it is obvious to this author that their primary function is most probably one of concealment, in that they very effectively trap sand particles and hold them in the grooves and excavations of the carapace, thus obscuring the crab's outline and allowing it to blend into the substrate. Such concealment would allow it to hide from predators and ambush prey as well. These sometime very ornate, even flower-like, surface structures might also aid in anchoring the crab in the substrate. They also undoubtedly have a structural advantage in their reinforcement of the carapace. Serène (1954) elaborates on their development and Guinot (1979) discusses their development and presents the hypothesis that they serve to channel water to the bases of the legs and that they aid in concealment as well. My own observations have indicated that their individual form can be species specific and therefore of particular use to paleontologists in the identification of crab fragments.

Subfamily Iliinae

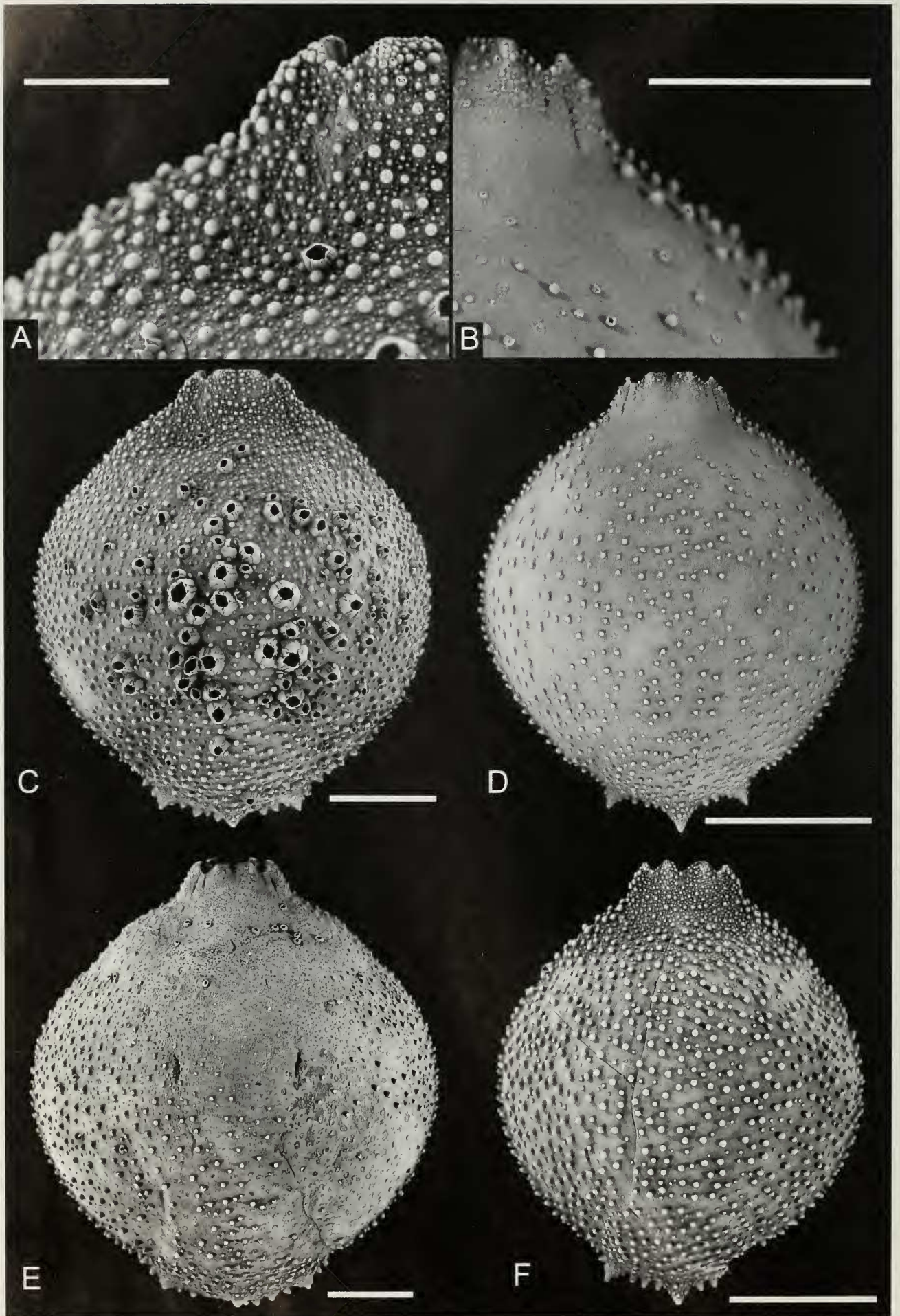
Genus *Persephona* Leach, 1817

Persephona niemeyeri, new species

Figs. 5A, C, E, F

Diagnosis.—Carapace hemispherical with three posterior spines; front bilobate, elevated, produced with orbits well beyond anterolateral margin; post frontal, hepatic and all other dorsal surfaces thickly covered with relatively high, subacute tubercles of various sizes; tubercles strongest along lateral and posterior margins, and highly concentrated on front, orbits and adjacent areas where developed into boletimorphs.

Description.—Carapace hemispherical, width about nine-tenths of length, regions



very weakly defined, front and orbits advanced well beyond anterolateral margins; posterior with three equally spaced recurved spines, two marginal, and one median above margin. Dorsal surfaces thickly covered with relatively high, subacute tubercles of various sizes; tubercles strongest along lateral and posterior margins, most concentrated below plural suture, where very low and closely spaced, and highly concentrated on front, orbits and adjacent areas where developed into bolitimorphs. Front very narrow, width about 0.09 width of carapace, bilobate, lobes separated by distinct v shaped sulcus, laterally defined by raised clusters of tubercles; anterior margins of lobes blunt, denticulate. Orbit very small, divided by three deep, narrow, open sutures creating four lobes. Minute, elongate tubercles span sutures from both sides, creating a pectinate appearance. Supraorbital eave and median lobe meet at a steep angle to form a broad v as seen from above. Large distinct bolitimorphs concentrated on outer lobe. Suborbital lobe with afferent channel below; channel deeply notched at anterolateral angle, inner angle rounded distally, margin pustulose and channel produced beyond front and orbits as seen in dorsal view. Hepatic region slightly swollen, weakly defined, thickly covered with tubercles. Superior margin of subhepatic region with low ridge of concentrated tubercles; ridge not joining but rather descending just below tubercles of anterolateral margin. Anterior and posterior lateral margins of carapace continuous, defined by a row of larger tubercles beginning at orbit and continuing along upper edge of plural suture to a point just above tooth of posterolateral angle; row poorly separated from dorsal tu-

bercles, sometimes indistinct or appearing as double row where intermixed with dorsal tubercles; area below plural suture covered with closely spaced low tubercles, surface appearing very rough, bordered below by distinct row of strong tubercles just above bases of ambulatory legs. Posterior margin slightly more than one-third carapace width, produced posteriorly, laterally defined by a broad, stout, triangular, acute recurved spine at each corner; margin between spines comprised of from seven to 10 large recurved tubercles; intestinal margin above with a single medially placed, stout, recurved spine. Spines coarsely granulate. Posterior gastric pits not evident.

Color.—Reddish orange to yellow when dry.

Etymology.—This species is named for Antonio B. Niemeyer, Jr., science teacher, retired, of Chesapeake, Virginia, in recognition of his contribution to science through his many years of teaching science in the public schools of tidewater Virginia and for the fundamentals of general science that he instilled in this author so many years ago.

Holotype.—The Lone Star Lakes, near Chuckatuck, Suffolk, Virginia. USGS 26891, (USNM 520710) cl 52.30 mm, cw 48.13 mm; *Paratypes:* (USNM 520711) cl 43.69 mm, cw 38.85 mm, USGS 26891 as above; (USNM 520712) cl 30.06 mm, cw 25.91 mm, USGS 26891 as above; (USNM 520713) cl 23.02 mm, cw 18.07 mm. Fragment of anterior portion of carapace only. USGS 26891 as above; (VMNH I3549) cl 36.83 mm, cw 33.27 mm. Same geographic locality as USGS 26891 above.

Occurrence.—The Lone Star Lakes, near Chuckatuck, Suffolk, Virginia.

Remarks.—Recent comparisons: *Perse-*

←

Fig. 5. *Persephona niemeyeri* Paratype (USNM 520711) A. closeup of left anterior surface in dorsal view. Scale = 4 mm. *Persephona rodesae* Holotype (USNM 520714) B. closeup of right anterior surface in dorsal view. Scale = 5 mm. *Persephona niemeyeri* Paratype (USNM 520711) C. dorsal view. Scale = 10 mm. *Persephona rodesae* Holotype (USNM 520714) D. dorsal view. Scale = 10 mm. *Persephona niemeyeri* Holotype (USNM 520710) E. dorsal view of geronic specimen, bare areas are a result of wear and abrasion. Scale = 10 mm. *Persephona niemeyeri* Paratype (USNM 520712) F. dorsal view. Scale = 10 mm.

phona niemeyeri is most similar to the Recent western Atlantic purse crab, *P. mediterranea* (Herbst, 1794) (see: Williams 1984 for synonymy) from which it can be immediately separated on the basis of its dense tuberculate covering alone.

Fossil comparisons: *Persephona niemeyeri* most closely resembles *P. rodesae* described below from which it can be separated as follows: 1.) *Persephona niemeyeri* has far more dorsal tubercles than *P. rodesae*, especially anteriorly on the postfrontal, frontal, and orbital surfaces; 2.) these tubercles are much higher and more acute than those of *P. rodesae*; 3.) the densely tuberculate hepatic region of *P. niemeyeri* differs considerably from that of *P. rodesae* which possesses only a few tubercles; and 4.) the lateral row of tubercles just above the plural suture of *P. niemeyeri* is poorly separated from the dorsal tubercles with which it inner grades, whereas this row in *P. rodesae* is well separated from the dorsal tubercles.

Specimens of isolated "arms" referred to *P. punctata* (Linné, 1758) by Rathbun (1935:106), from her Virginia localities will probably, in time, be shown to represent *P. niemeyeri* and/or *P. rodesae*. The right posterior spine of paratype (USNM 520712) was broken off prior to photography but has since been restored. The barren surfaces seen on the figure of the holotype (USNM 520710) of *P. niemeyeri* are the apparent result of abrasion on this gerontic specimen. Remnants of the dense covering of these tubercles and bolitimorphs can be seen on the actual specimen.

***Persephona rodesae*, new species**

Fig. 5B, D

Diagnosis.—Carapace hemispherical with three posterior spines; front bilobate, elevated, produced with orbits well beyond anterolateral margin; post frontal surface barren of tubercles, hepatic region and all other dorsal surfaces sparsely covered with relatively low, small, obtuse to subacute tu-

bercles of subequal size; tubercles strongest along lateral and posterior margins, and very small to minute where highly concentrated on distal surface of front, and around orbits.

Description.—Carapace hemispherical, width about nine-tenths of length, regions very weakly defined, front elevated, produced with orbits well beyond anterolateral margin; posterior with three equally spaced recurved spines, two marginal, and one median above margin. Dorsal surfaces sparsely covered with relatively low, blunt to subacute tubercles of subequal size; tubercles strongest along lateral and posterior margins, most concentrated below plural suture, where very low, rounded and closely spaced; very small to minute tubercles highly concentrated on front and orbits where some are developed into small bolitimorphs; post frontal surfaces and adjacent areas behind orbits nearly barren, void of tubercles. Front very narrow, width about 0.11 width of carapace, bilobate, lobes separated by distinct v-shaped sulcus, laterally defined by low ridge formed by raised clusters of tubercles; anterior margins of lobes blunt, denticulate. Orbit very small, divided by three deep, narrow, open sutures creating four lobes. Minute, elongate tubercles span sutures from both sides, creating a pectinate appearance. Supraorbital eave and median lobe meet at a steep angle to form a broad v as seen from above. A few very small bolitimorphs are present along margin of outer lobe and just posterior to orbit along anterolateral margin. Hepatic region slightly swollen, weakly defined, surface with only a few tubercles. Subhepatic region not preserved in type series. Anterior and posterior lateral margins of carapace continuous, defined by a distinct row of larger tubercles beginning at orbit and continuing along upper edge of plural suture to a point just above tooth of posterolateral angle; row of tubercles usually well ordered and well separated from dorsal tubercles, particularly anteriorly; posteriorly row may inner grade with some dorsal tubercles and appear as a

double row; area below plural suture covered with pavement of closely spaced low tubercles, surface appearing very rough. Posterior margin slightly more than one-third carapace width, produced posteriorly, laterally defined by a broad, stout, triangular, acute recurved spine at each corner; margin between spines comprised of from seven to 11 large recurved tubercles; intestinal margin above with a single medially placed, stout, recurved spine. Spines coarsely granulate. Posterior gastric pits not evident.

Color.—Pale yellow when dry.

Etymology.—This species is named for Mary Betty Rodes, science teacher, deceased, formerly of Portsmouth, Virginia, in recognition of her contribution to science through her many years of teaching science in the public schools of tidewater Virginia. In addition Miss Rodes provided the author with his first formal introduction to paleontology.

Holotype.—Rices Pit, Hampton, Virginia. USGS 26893, (USNM 520714) cl 27.05 mm, cw 23.86 mm. *Paratypes*: (USNM 520715) cl 32.05 mm, cw 28.39 mm, USGS 26893 as above; (USNM 520716) cl 32.60 mm, carapace incomplete, cw 35.50 mm, USGS 26893 as above; (USNM 520717) cl 15.47 mm, cw 16.41 mm, fragment of anterior portion of carapace only, USGS 26893 as above; (VMNH I3550) cl 27.88 mm, cw 24.95 mm, same geographic locality as USGS 26893 above.

Occurrence.—Rices Pit, Hampton, Virginia.

Remarks.—Recent comparisons: *Persephona rodesae* appears most similar to the Recent Western Atlantic purse crab, *P. mediterranea* (Herbst, 1794) (see: Williams 1984 for synonymy) from which it differs in having: 1.) relatively high, obtuse to subacute tubercles, compared to the very low rounded tubercles of *P. mediterranea*; 2.) small to minute tubercles concentrated on its front and orbits unlike *P. mediterranea* where these areas are all but barren; 3.) fewer, though stronger tubercles on its he-

patric region; 4.) fewer, though stronger tubercles along its lateral margins; 5.) a much rougher surface below its lateral margins; and 6.) far fewer and much stronger tubercles along its posterior border.

Fossil comparisons: *Persephona rodesae* most closely resembles *P. niemeyeri* described above. See remarks for *P. niemeyeri* for comparison.

Persephona rodesae and *P. niemeyeri* have not been found at the same locality or in similar sediments. *Persephona rodesae* has been found in the shelly sands of Rices Pit, a much calmer, much less violent environment during its deposition than that seen at the Chuckatuck Bar where *P. niemeyeri* is found. The morphological differences between these two species therefore appear directly related to these environmental differences.

Family Majidae

Subfamily Inachinae

Genus *Euprognatha* Stimpson, 1871

Euprognatha ricei, new species

Fig. 6

Diagnosis.—Carapace pyriform in outline, surface with five unusually long narrow blunt spines, mesogastric and cardiac spines longest, surface between base of mesogastric spine and protogastric regions exhibiting a distinct, pentagonal array of granulations mimicking the shape of a royal crown; intestinal spine present, well developed; interantennular spine absent.

Description.—Carapace pyriform in outline; fronto-orbital region strongly projecting, narrow, occupying less than one-fourth width of carapace; regions well defined, moderately swollen. Front bidentate, projecting; projections represent superior surface of "shoe-shaped" antennal fossae below; projections broadly triangular or obtuse distally, divided by a shallow sulcus extending posteriorly where terminating at an inverted v-shaped row of eight granules. Orbit circular, margins vertical, subparallel; supraorbital eave covered with triangular

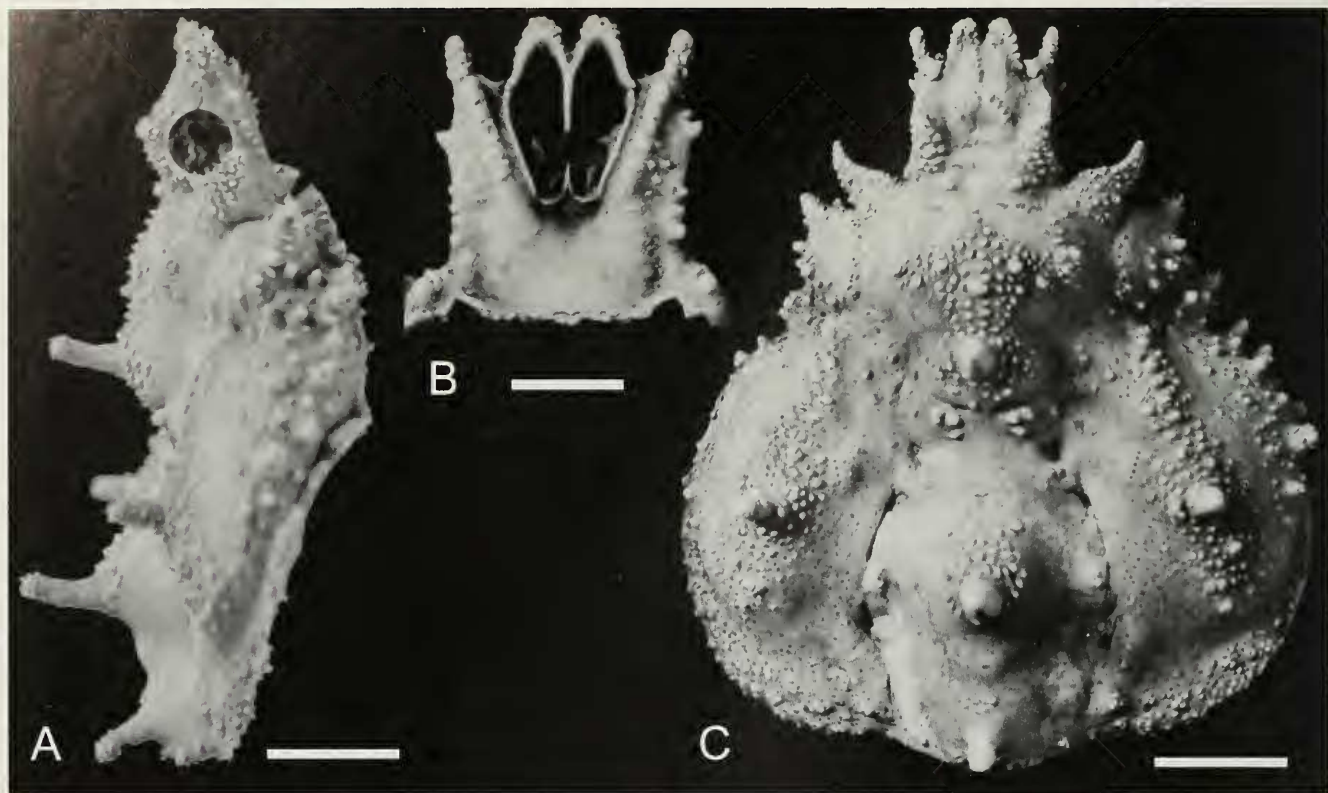


Fig. 6. *Euprognatha ricei* Holotype (USNM 520718) A. right lateral view. Scale = 2 mm. B. ventral closeup of antennule fossae, and long basal segment of antenna. Scale = 1 mm. C. dorsal view. Scale = 2 mm.

field of granules posteriorly; point of field distal where defined by a strong tubercle on orbital margin. Eyes apparently on long stalks, resting within depression of postorbital spine. Postorbital spine very strong; broad basally, tapering to a point distally, obliquely directed forward. Basal antennal article with inner and outer rows of granules of which several are developed into short, obtuse spines (tubercles); article directed only slightly obliquely forward, terminating in a granulated spine subequal in advancement to the front. Antennal sternum weak, not produced; interantennular spine absent. Outer margin of pterygostomial region with rows of coarse granules; superior row with large blunt tooth posteriorly. Buccal cavity broadest anteriorly, lateral margins divergent, width about one-third width of carapace. Hepatic region conical, sparsely covered with rounded granules or small tubercles, terminating obliquely in a strong blunt spine; spine produced laterally to a distance subequal to advancement of postorbital spine. Mesogastric, cardiac, intesti-

nal, and branchial regions each surmounted with a single prominent cylindrical blunt spine; mesogastric spine longest, vertically directed; cardiac spine subequal to mesogastric spine, slightly directed posteriorly; intestinal and branchial spines much shorter and of subequal length; the former obliquely directed posteriorly; latter obliquely directed laterally. Spines smooth laterally with their distal ends granulated. Surface of carapace noticeably punctate, otherwise relatively smooth except for concentrations of low tubercles or rounded granules along frontal margins, supraorbital eaves, postorbital spines, hepatic regions, lateral margins, and bases of prominent spines. Irregular concentrations of tubercles and granules appearing as a distinct anteriorly directed row on each branchial region; row beginning just posterior to prominent spine of branchial region and converging anteriorly where tapering to a point at branchial-hepatic junction. Surface between base of mesogastric spine and protogastric regions defined by a very distinct pentagonal array

of granulations arranged in the shape of a royal crown. Tubercles strongest on or near hepatic and anterolateral margins. Posterior gastric pits distinct, close set at base of mesogastric region, each bounded posteriorly by cluster of three granules. Distinct broad, smooth, groove separating cardiac and intestinal regions from branchial region.

Branchial region posterolaterally produced into a relatively wide, flattened, granulated margin. Posterior margin moderately produced posteriorly, width about one-third carapace width.

Color.—Ash white when dry, or gray when wet.

Etymology.—This species is named in honor and appreciation of Mr. William M. Rice, deceased, of Hampton, Virginia, who allowed the author unrestricted access to his borrow pit and who, with his wife, Madeline, and family built a museum on his property for the purpose of educating students in the Hampton Roads area. This small museum, known as The Kenneth E. Rice Memorial Museum (after his youngest son), the borrow pit behind it, and the tutorage of Mr. Rice served more than five thousand students of all ages each year. His positive impact on the paleontology of the area is unsurpassed.

Holotype.—Rices Pit, Hampton, Virginia. USGS 26893, (USNM 520718) cl 10.31 mm, cw 9.01 mm. *Paratypes*: (USNM 520719) cl 4.41 mm, cw 3.46 mm, USGS 22209 same geographic locality as USGS 26893 above; (VMNH I3551) cl 7.75 mm, cw 6.83 mm, USGS 26893 as above.

Occurrence.—Rices Pit, Hampton, Virginia.

Remarks.—Recent comparisons: Of the known living species of *Euprognatha*, *E. ricei* appears most similar in overall form, number and placement of prominent dorsal spines and distribution of tubercles and granules to *E. gracilipes* A. Milne-Edwards, 1878b (Florida Keys to Barbados, Rathbun 1925). *Euprognatha ricei* can however be easily separated from *E. gracilipes* as follows: 1.) the prominent spines

of *E. ricei* are much longer than those of *E. gracilipes* and *E. ricei* unlike *E. gracilipes* possesses an intestinal spine; and 2.) the dorsal surface of *E. ricei* is much less granulate than the evenly, coarsely granulated surface of *E. gracilipes*. The presence of long mesogastric, branchial, and cardiac spines, and in particular a long intestinal spine in combination with its sparsely granulated surface, the absence of an interantennular spine and the presence of a pentagonal array of granules in the shape of a royal crown on its mesogastric region easily separate *E. ricei* from all other living species of *Euprognatha*.

Fossil comparisons: Rathbun (1935) identified two left dactyls from the Miocene of Liberty County, Florida as *Euprognatha* sp., p. 112, pl. 24, figs. 16–19. Lacking associated chela, the type specimens of *E. ricei* cannot be compared with Rathbun's material.

The distal end of the left basal antennal article was broken and lost by the author in handling the specimen after the photograph was completed.

Subfamily Mithracinae

Genus *Stenocionops* Desmarest, 1823

Stenocionops dyeri, new species

Fig. 7

Diagnosis.—Carapace oblong-ovate, strongly arched anteriorly; superior lateral marginal spines three; frontal depression laterally bordered by 10 to 18 small spines; cardiac region greatly elevated, armed with an irregular pentagonal array of five short spines.

Description.—Carapace oblong-ovate, strongly arched anteriorly, surface uneven, regions well defined. Length from rostral notch along middorsal line from 1.33 to 1.41 times greatest width, broadest across middle of branchial regions; greatest height approximately one-half that of width. Rostral horns basally divergent, laterally subparallel, short, flattened, slightly upturned distally. Frontal depression deep, ovate, lat-

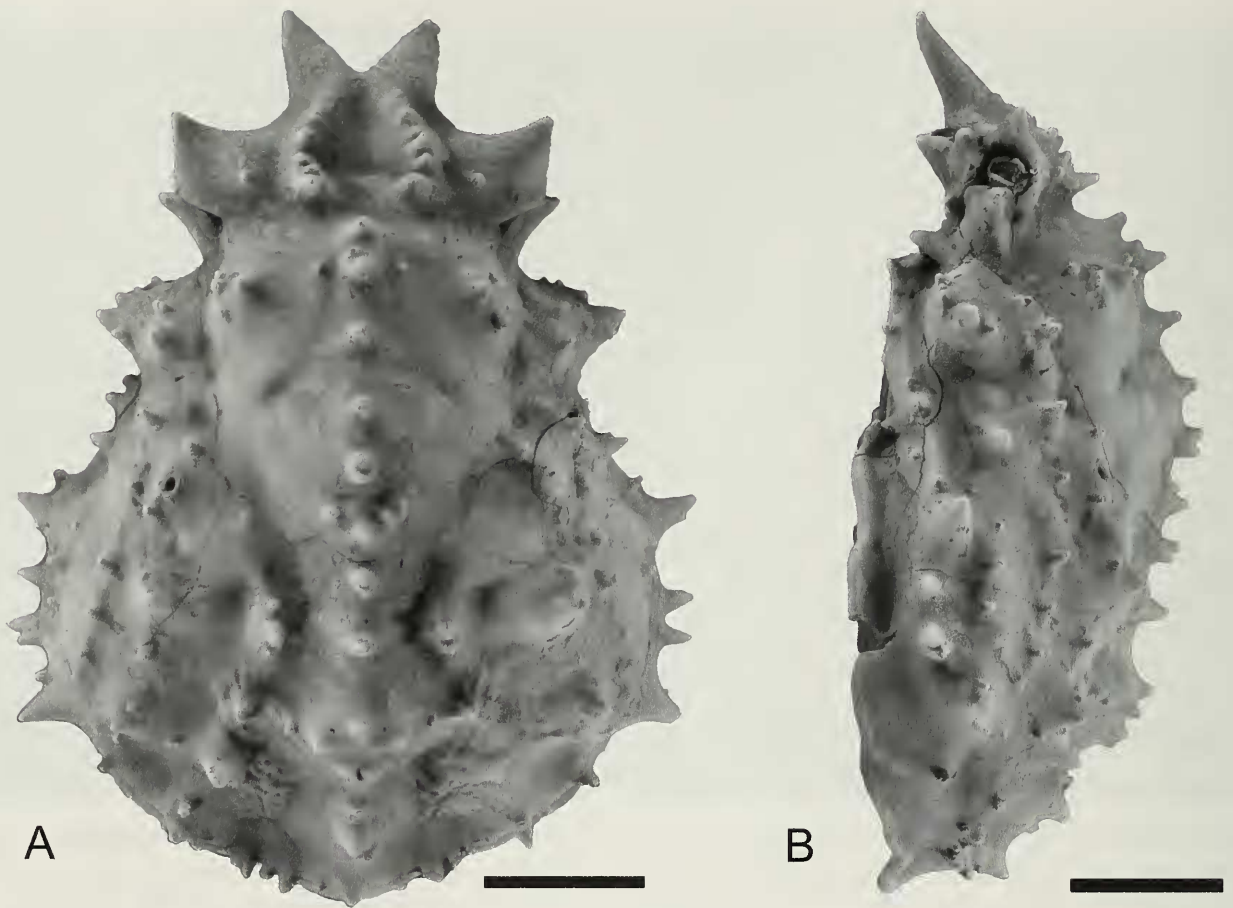


Fig. 7. *Stenocionops dyeri* Holotype (USNM 520720) A. dorsal view and B. left lateral view. Scale = 10 mm.

erally bordered by 10 to 18 small spines decreasing in height anteriorly. Fronto-orbital region broad, more than one-half times that of width; orbits strongly projecting. Eyes small, retractable within deep tubular orbits; preocular spine superior, a small distinct spine or tubercle medial to its base; postocular spine smaller, acute. Orbit completed below by a blade-like lateral expansion of basal antennal article. Basal antennal article broader than long, armed with 3 spines, one anterior-external, short, acute, barely visible dorsally; another, posterior-external, usually very weak; and last, anterior-internal, strong, acute, extending forward and obliquely downward from basal insertion of second antennal article. Second antennal article not extending forward to or beyond rostral notch. Opening of green gland oval, noticeably raised, a prominent, obliquely downward-directed, acute spine near its external-lateral border. Pterygosto-

mian region triangular, armed with two small outer marginal spines; anterior longest. Inner margins raised, rim like, anteriorly terminated by an anvil-like process. Buccal frame broader than long, widest anteriorly; width about one-third width of carapace width. Superior lateral marginal spines three; one hepatic and two branchial. Secondary lateral marginal spines common, may exceed ten, their number apparently increasing with age. Hepatic region swollen, very distinct, reaching beyond fronto-orbital width, armed laterally with a cluster of five or more spines; superior inner margin with two spines, posteriormost longest and strongest. Mid-dorsal line slightly raised, ridge-like. Gastric region greatly arched anteriorly; armed with from eight to 10 short spines, of which four are usually mesogastric, two metogastric, and three urogastric. Posterior gastric pits faint, bordered by

curved row of spines just distal to cervical groove.

Cardiac region greatly elevated, usually armed with a characteristic irregular pentagonal array of five small spines, posteriormost two, often close set. Cardio-intestinal and metabranchial regions separated by deep furrows. Intestinal region armed with two distinct spines along midline, posteriormost largest; spines aligned perpendicular to a lower horizontal row of from two to five smaller spines and/or tubercles, their number apparently decreasing with age; row of spines bordered below by wide, shallow sulcus. Posterior margin rounded, narrow, slightly projecting, width less than one-half fronto-orbital width. Branchial regions uneven, moderately spinous. A distinct, armed, broadly conical prominence on each epibranchial, mesobranchial and metabranchial region, which when roughly aligned with rostral notch, forms an inverted V of approximately 30°. Epibranchial prominence usually with two secondary spines or tubercles. A prominent ridge armed with three low spines, posterior longest, occupying inter-lateral margin of metabranchial region.

Lower margin of entire carapace terminating in a rounded rim. Entire surface of body (chelipeds—excepting distal half of fingers) closely covered with minute, circular pores.

Coxa, basis, and ischium of chelipeds and ambulatory legs, unarmed. Merus of cheliped quadrangular in section, armed with four distinct lateral rows of spines, the dorsal row being most prominent with four superior spines and as many as five smaller spines or tubercles. Carpus smooth. Hand elliptical in section, highest proximally, smooth to finely granulate. Fingers less than one-half length of palm, not gaping. Ambulatory legs circular in section; merus of first and second pair moderately tuberculate above; third and fourth pairs smooth. Legs decreasing in length posteriorly.

Color.—Ash white with faint patches of pink when dry, gray when wet. Some living

species of *Stenocionops* are dark red, such as *Stenocionops furcata coelata* (A. Milne-Edwards, 1878a). See Williams (1984:339).

Etymology.—This species is named for Brian J. Dyer, microbiologist, Old Dominion University, Norfolk, Virginia for his contribution to science through his years of research and teaching and especially for his years of encouragement and field assistance to the author.

Holotype.—The Lone Star Lakes, near Chuckatuck, Suffolk, Virginia. USGS 26891, (USNM 520720) cl including rostrum 58.38 mm, excluding rostrum 54.47 mm, cw including spines 44.65 mm, excluding spines 40.03 mm. *Paratypes*: (USNM 520721) Female: cl including rostrum 53.91 mm, excluding rostrum 49.96 mm, cw including spines 41.70 mm, excluding spines 37.72 mm, right propodus: prl 21.63 mm, prh 6.09 mm, prl 3.15 mm, left propodus, prl 20.96 mm, prh 5.13 mm, prt 3.22 mm, USGS 26891 as above; (VMNH I3552) cl including rostrum 42.95 mm, excluding rostrum 39.21 mm, cw including spines 32.22 mm, excluding spines 27.75 mm, same geographic locality as USGS 26891 above.

Occurrence.—The Lone Star Lakes, near Chuckatuck, Suffolk, Virginia.

Remarks.—Recent comparisons: *Stenocionops dyeri* appears most similar in shape and overall character to *S. spinosissima* (Saussure, 1857) from which it can be easily separated as follows: 1.) *Stenocionops dyeri* has three strong lateral spines compared to the five found in *S. spinosissima*; 2.) *S. dyeri* has short, flattened rostral horns compared to the much longer, more acute horns of *S. spinosissima*; and 3.) *S. dyeri* has between 13 to 15 short median spines, of which those on the cardiac region are arranged in an irregular pentagonal array in contrast to *S. spinosissima* which exhibits 10 median spines of which only two are found on the cardiac region. *Stenocionops dyeri* also superficially resembles a much smaller species of *Stenocionops*, *S. triangulata* (Rathbun, 1892) which also possess-

es three lateral spines. These spines in *S. dyeri*, however, are shorter and much less acute. *Stenocionops dyeri* also differs from this species in having: 1.) much flatter, shorter and less divergent rostral horns; 2.) 13 to 15 median spines compared to about nine on *S. triangulata*; and 3.) an irregular pentagonal array of five spines on its cardiac region compared to only one or two on this region in *S. triangulata*. In reference to *S. triangulata*, Rathbun (1925:461) states: "Known only from small and immature specimens". The pentagonal array of spines on the cardiac region of *S. dyeri* alone sets it apart from all other known species of *Stenocionops*.

Fossil comparisons: Rathbun (1935) described *Stenocionops primus* from the Upper Cretaceous Brownstown Formation, of Howard County, Arkansas and *Stenocionops suwanneeana* from the Eocene Ocala Limestone of Suwannee County, Florida. The chela of these two species may indeed resemble those of adult males of *Stenocionops* or other mature majid chela but in size and coarse granulation they are very different from the nearly smooth diminutive female chela of *S. dyeri*. The chela in both adult male and female species of some living representatives of *Stenocionops* are relatively small, like those of *S. dyeri*, but in reaching maturity the chela in gerontic males can become quite large. The geologic time difference between *S. dyeri* and these geologically much older taxa is such that it would be very unlikely that they represent the same species.

The barnacle, *Balanus* sp., is often found completely covering the dorsal surface of the carapace of *S. dyeri* where it apparently lived as a symbiont during the life of the crab. This barnacle has not yet been found covering the orbital openings of this crab, thus revealing that the crab was indeed alive and able to keep its orbits clear during this relationship. The massive numbers of this barnacle found on some specimens of *S. dyeri* greatly increased the crab's surface area and undoubtedly contributed to its be-

ing washed about and buried in the Chuckatuck Bar deposits by strong currents during storms. These same barnacles also strengthened the dorsal aspect of the carapace allowing it to be preserved in this high energy environment of deposition.

Acknowledgments

Mr. H. B. Roberts, deceased, formerly of the Department of Invertebrate Zoology, NMNH, SI, correctly identified *Hepatus bottomsii*, *Persephona rodesae*, *Euprognatha ricei* and *Stenocionops dyeri* as new in a letter to the present author, dated 13 October 1964. Given the incomplete and often fragmentary nature of the material presented to him at that time, his identifications are remarkable for their accuracy, a testament to his knowledge and ability. Due to his declining health, Mr. Roberts was unable to pursue descriptions of these and other new taxa (see: Manning & Blow 1980, Blow & Bailey 1992) and passed that task on to this author before his retirement in June 1973. He died 14 March 1979.

I thank E. E. Bottoms for introducing me to a number of fossil decapod localities in the Hampton Roads area in the fall of 1962, and for years of cooperative fieldwork and mutual assistance. I particularly thank my parents, R. V. and C. D. Blow, for years of logistical support, field assistance, and for their own collecting efforts which have benefitted and continue to benefit my research these past 40 years. Mr. W. A. Staylor, Mr. H. F. Saunders and the other men and women of the Lone Star Cement Co. kindly allowed the author unrestricted access to their diggings. R. H. Bailey, B. A. Bedette, B. J. Dyer, L. W. Ward, and the late D. Wilson helped the author in the field on a number of occasions, adding their expertise and collections to the research and writing of the present paper. L. D. Campbell and Svein Nielsen kindly made their collections available to the author for study.

I thank S. Whittaker, of the SEM lab, Smithsonian Institution, for providing the

photomicrographs of *P. baileyi*, M. G. Harsewych for providing the digital images of the remaining taxa except for the dorsal and lateral views of *E. ricei*, which were taken by Mr. T. F. Phelan. My sincere thanks to J. A. Sanner for enhancing the images in Adobe Photoshop and constructing the finished digital plates. In addition B. A. Bedette read the manuscript and offered numerous suggestions and corrections. T. R. Waller provided space in his laboratory, and scientific and editorial advice throughout the preparation of this manuscript.

Literature Cited

- Bell, T. 1855. A Monograph of the Leucosiadae, with observations on the relations, structure, habits, and distribution of the family; a revision of the generic characters; and descriptions of new genera and species. *Horae Carcinologicae, or Notices of Crustacea*, I.—Transactions of the Linnean Society 21:277–314 + pls. 30–34.
- Blow, W. C., & R. H. Bailey. 1992. *Chasmocarcinus robertsi*, a new crab species from the Miocene of Virginia, with notes on the genus *Falconoplax* (Crustacea, Decapoda, Goneplacidae).—Tulane Studies in Geology and Paleontology 25(4):175–185.
- Campbell, L. D. 1993. Pliocene molluscs from the Yorktown and Chowan River Formations in Virginia.—Virginia Division of Mineral Resources Publication 127:1–259.
- Collins, J. S. H., & S. F. Morris. 1976. Tertiary and Pleistocene crabs from Barbados and Trinidad.—Palaeontology 19(1):107–131.
- Desmarest, A. G. 1823. Malacostracés. Pp. 158–425 in *Dictionnaire des Sciences Naturelles*, vol. 28. Strasbourg.
- Gibson, T. G. 1967. Stratigraphy and paleoenvironment of the phosphatic Miocene strata of North Carolina.—Geological Society of America Bulletin 78(5):631–650, pls. 1, 2.
- Guinot, D. 1979. Morphologie et phyogenèse des Brachyours.—Mémoires du Muséum national d'Histoire naturelle (Paris), new series A (zoology) 112:1–354.
- Haj, A. E., & R. M. Feldmann. 2002. Functional morphology and taxonomic significance of a novel cuticular structure in Cretaceous raninid crabs (Decapoda: Brachyura: Raninidae).—Journal of Paleontology 76(3):472–485.
- Hazel, J. E. 1971a. Ostracode biostratigraphy of the Yorktown Formation (upper Miocene and lower Pliocene) of Virginia and North Carolina.—Geological Survey Professional Paper 704:1–13.
- . 1971b. Paleoclimatology of the Yorktown Formation (upper Miocene and lower Pliocene) of Virginia and North Carolina: Pp. 361–375 in H. J. Oertli, ed., *Paléoécologie Ostracodes*, Pau, 1970.—Bulletin Centre Recherche Pau-SNPA, 953 pp., 3 tab.
- Herbst, J. F. W. 1794. Versuch einer Naturgeschichte der Krabben und Krebse, nebst einer systematischen Beschreibung ihrer verschiedenen Arten 2(5):147–162 + pls. 37–40.
- Johnson, G. H. 1969. Guidebook to the geology of the York-James Peninsula and south bank of the James River.—College of William and Mary Department of Geology Guidebook No. 1. Atlantic Coastal Plain Geological Association, Tenth Annual Field Conference and First Annual Geological Field Conference: 1–33.
- , & N. K. Coch. 1969. A Coquina facies in the Yorktown Formation near Chuckatuck, Virginia and its geological implications.—(Abs.) Geological Society America Special Paper 121: 448.
- Kier, P. M. 1972. Upper Miocene echinoids from the Yorktown Formation of Virginia and their environmental significance.—Smithsonian Contributions to Paleobiology 13:1–41. Smithsonian Institution Press, Washington.
- Latreille, P. A. 1802. Histoire naturelle générale et particulière des Crustacés et des Insectes 3:13–467. Paris.
- Leach, W. E. 1817. Malacostraca Podophthalma Britannia; or descriptions of the British species of crabs, lobsters, prawns, and of other Malacostraca with pedunculated eyes. James Sowerby. London, XIV, 5 p., unpagged + pls 16, 25 and 44.
- Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, 10th edition. Laurentius Salvius. Stockholm 1:1–824.
- Manning, R. B., & W. C. Blow. 1980. Henry B. Roberts 1 September 1910–14 March 1979.—Crustaceana 39(1):104–107, pl. 1.
- Mansfield, W. C. 1943 [1944]. Stratigraphy of the Miocene of Virginia and the Miocene and Pliocene of North Carolina. Pp. 1–19 in J. Gardner, ed., *Mollusca from the Miocene and Lower Pliocene of Virginia and North Carolina: Pt 1, Pelecypoda*.—U.S. Geological Survey Professional Paper 199-A:1–178.
- Milne-Edwards, A. 1865. Description de quelques Crustacés nouveaux on peu connus de la famille des Leucosiens.—Annales Société Entomologique de France 4(5):148–159, pl. 6.
- . 1878a. Note sur quelques Crustacés nouveaux

- appartenant au groupe des Oxyrhynques.—Bulletin de la Société Philomathique de Paris 7(2): 222–225.
- . 1878b. Études sur les Xiphosures et les Crustacés de la Région Mexicaine.—In Mission Scientifique au Mexique et dans l'Amérique centrale part 5(4):121–184, pls. 21–27, 29–30.
- . 1880. Études préliminaires sur les Crustacés, 1^{ere} partie. In reports on the results of dredging under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877, '78, '79 by the U.S. Coast Survey Steamer "Blake," Lieut. Commander C. D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., Commanding.—Bulletin of the Museum of Comparative Zoölogy at Harvard College 8(1): 1–68, pls. 1, 2.
- , & E. L. Bouvier. 1894. Brachyures et Anomoures. In Crustacés décapodes provenant des campagnes du yacht l'Hirondelle (1886, 1887, 1888), Première Partie. Résultats des Campagnes Scientifiques accomplies sur son yacht par Albert 1^{er}, Prince Souverain de Monaco 7:1–112, pls. 1–11.
- , & E. L. Bouvier. 1902. Les Dromiacés et Oxystomes. In reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78), in the Caribbean Sea (1878–79), and along the Atlantic Coast of the United States (1880), by the U. S. Coast Survey Steamer "Blake", Lieut. Com. C. D. Sigsbee, U. S. N., and Commander J. R. Bartlett, U. S. N., Commanding, XXXIX.—Memoirs of the Museum of Comparative Zoölogy at Harvard College 27(1):1–127, pls. 1–25.
- Milne-Edwards, H. 1834. Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux 1:1–468. Paris.
- Pennant, T. 1777. Crustacea, Mollusca, Testacea. British Zoology, edition 4, 4:London, 1–154, pls. 1–93.
- Rathbun, M. J. 1892. Catalogue of the crabs of the family Periceridae in the U.S. National Museum.—Proceedings of the United States National Museum 15(901):231–277, pls. 28–40.
- . 1896. The genus *Callinectes*.—Proceedings of the United States National Museum 18(1070): 349–375, pls. 12–28.
- . 1925. The spider crabs of America.—United States National Museum Bulletin 129:1–613, pls. 1–283.
- . 1926. The fossil stalk-eyed Crustacea of the Pacific slope of North America.—United States National Museum Bulletin 138:1–155, pls. 1–39.
- . 1935. Fossil Crustacea of the Atlantic and Gulf Coastal Plain.—Geological Society of America, Special Papers 2:1–160, pls. 1–26.
- . 1937. The Oxystomatous and allied crabs of America.—United States National Museum Bulletin 166:1–278, pls. 1–86.
- Saussure, H. de. 1857. Diagnoses de quelques Crustacés nouveaux de l'Amérique tropicale.—Revue et Magzin de Zoologie Pure et Appliquée, 2(9):501–505.
- Serene, R. 1954. Sur quelques especes rares de Brachyures (Leucosidae) de l'Indo-Pacifique.—Trebhina 22(3):453–499, pls. 7–10.
- Stimpson, W. 1859. Notes on North American Crustacea, No. 1.—Annals of the Lyceum of Natural History of New York 7(1862)(2):49–93, 1 plate.
- . 1871. Preliminary report on the Crustacea dredged in the Gulf Stream in the Straits of Florida, by L. F. de Pourtales, Assistant United States Coast Survey. Part 1. Brachyura.—Bulletin of the Museum of Comparative Zoology at Harvard College 2(2):109–160.
- Verrill, A. E. 1869. On the parasitic habits of Crustacea.—American Naturalist 3:239–250. [*HepateLLa amica* Smith described as footnote p. 250]
- Ward, L. W., & B. W. Blackwelder. 1980. Stratigraphic revision of Upper Miocene and Lower Pliocene beds of the Chesapeake Group, Middle Atlantic Coastal Plain.—Contributions to Stratigraphy, Geological Survey Bulletin 1482-D:1–61, pls. 1–5.
- , & N. L. Gilinsky. 1993. Molluscan assemblages of the Chowan River Formation, Part A, Biostratigraphic analysis of the Chowan River Formation (Upper Pliocene) and adjoining units, The Moore House Member of the Yorktown Formation (Upper Pliocene) and the James City Formation (Lower Pleistocene).—Virginia Museum of Natural History Memoir 3, Part A: 1–32, plate 1. Tables 1, 2, & 4–6 & fig. 6 not paginated (in pocket).
- Williams, A. B. 1965. Marine decapod crustaceans of the Carolinas.—Fishery Bulletin 65(1):1–298.
- . 1984. Shrimps, lobsters, and crabs of the Atlantic Coast of the eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, D.C., 550 pp.

Appendix 1

Locality register

- USGS 26891 The Lone Star Lakes, formerly Lone Star Cement Company open-pit mine, about 1 km north of Chuckatuck, Suffolk, Virginia. USGS Chuckatuck, 7½-minute quadrangle map, 1965 photorevised 1979.
- USGS 26892 Open-pit mine, locally known as Riddick Pit, about 4.4 km southeast of Benns Church, on east side of Va. route 10/32, Isle of Wright County, Virginia. USGS Benns Church 7½-minute quadrangle map, 1965 photorevised 1986.

USGS 26893 Rices Pit belonging to Mr. William M. Rice, about 0.4 km north of intersection of Fox Hill Road (Rte. 167) and Harris Creek Road, Hampton, Virginia. USGS Hampton, 7½-minute quadrangle map, 1965 photorevised 1986.

USGS 22209 Same geographic locality as 26893 above but collected by a large group of Smithsonian scientists lead by G. A. Cooper in 1966.